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# Spatial and temporal variation in tree seed production and dispersal in a New Zealand temperate rainforest

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**Abstract.** Spatial and temporal variation in tree seed production is an important driver of the population dynamics of trees and of mammalian and avian seed consumers. Many studies have documented strong synchrony in production of intermittent large tree seed crops (masting), with cascading effects on the food webs of seed consumers and their predators. We used inverse modeling to characterize spatial and temporal variation in seed production and dispersal by four dominant tree species (two angiosperms and two conifers) over 8 years in southern temperate rainforests of New Zealand. In contrast to expectations from masting theory, there was little evidence of synchrony across species in years of high seed production, and only weak evidence in support of the expectation that temporal variation in seed production within species was strongly bimodal. Contrary to expectation from allometric scaling rules, there was no increase in reproductive effort once tree size (DBH) exceeded a minimum threshold (22–29 cm DBH) in the two angiosperm species. In the conifers, the minimum estimated size threshold for seed production was much higher (42–56 cm DBH), and in one of the species increased faster than linearly with biomass above the threshold size, indicating that the very largest trees in the conifer populations dominated seed production. Of the two species that occurred commonly on both fertile alluvial sites and less fertile uplifted marine terraces, the angiosperm species had higher per capita seed production on the fertile sites, while the conifer had higher per capita seed production (during seed years) on the less fertile sites. Local seed rain from all four species declined steeply with increasing distance from a parent, with peak local dispersal within 6 m of parent trees. This is not surprising given that the species are predominately gravity or animal dispersed with poor adaptations for wind dispersal. A substantial fraction of the input of seeds of all four species could not be attributed to local parent trees, consistent with longer distance dispersal by animals.

**Key words:** *Dacrydium cupressinum;* inverse modeling; masting; New Zealand; *Nothofagus menziesii; Nothofagus solandri* var. *cliffortioides*; *Podocarpus hallii;* seed dispersal; seed production; temperate rainforest.

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## INTRODUCTION

Spatial and temporal variation in seed rain in forests is an important driver of plant and animal dynamics (Jensen 1982, Ostfeld and Keesing 2000). While many pioneer species have adaptations for long distance dispersal, seeds of many other tree species have mean dispersal distances

of only 10–50 m (Ribbens et al. 1994, Clark et al. 1999). This limited dispersal may act to promote coexistence among late successional tree species (Pacala et al. 1996). There is also ample evidence of considerable temporal variation in seed production by tree species (Norton and Kelly 1988, Allen and Platt 1990, Richardson et al. 2005). The synchronous but intermittent mass production of seed by a given species (i.e., masting) at a regional scale is often invoked as a strategy evolved to overwhelm consumption by seed predators (Janzen 1971, Silvertown 1980, Kelly and Sork 2002), or to increase the effectiveness of pollination (Herrera et al. 1998, Kelly et al. 2001). Individual reproductive effort is typically assumed to be a function of a plant's biomass, according to allometric scaling rules (Niklas 1993), although many studies report that not all individuals in a population contribute large seed crops at each 'mast' event (Herrera et al. 1998, Connell and Green 2000).

Large irregular seed crops represent an important pulsed resource for birds, insects and mammals (Jensen 1982, Pucek et al. 1993, Fitzgerald et al. 1996, Pech et al. 1999, Choquenot and Ruscoe 2000). In New Zealand, these high seedfall events result in a cascade of responses by both native birds and insects, and introduced mammals (Ruscoe et al. 2005*b*, Kelly et al. 2008). Rodents respond numerically to large seedfall events (Ruscoe et al. 2004, Ruscoe et al. 2005*b*) and drive increases in mustelid populations (King 1983). Both rodents and mustelids are predators of native bird and insect species and these 'mast' seeding events result in increased predation (O'Donnell and Phillipson 1996, Ruscoe et al. 2005*a*). While there are differences in preference of the rodent seed predators for different species of tree seeds, the consumers are generalists rather than specialists (Murphy 1992, Ruscoe et al. 2004, Grant-Hoffman and Barboza 2010), and thus the overall impact of tree seed production on the dynamics of both the seed consumers and their mustelid predators needs to be examined in the community-level context of synchrony of seed production across species as well as within species.

There have been three general approaches to characterizing seed production and dispersal around parent trees (Nathan and Muller-Landau 2000, Greene and Calogeropoulos 2002): (1) direct measurements of seed rain around isolated individuals (i.e., Kitajima and Augspurger 1989), (2) development of theoretical models based on the mode of dispersal and the properties of the propagules and the dispersing agents (reviewed in Turchin 1998), and (3) neighborhood analysis using inverse modeling to estimate the parameters of the dispersal functions, based on measurements of seed rain or seedlings at given locations and a map of the distribution and sizes of the potential parent trees (Ribbens et al. 1994, Clark et al. 1999, LePage et al. 2000). A fourth approach is emerging, using genetic markers to identify maternal trees for seeds sampled at known locations in mapped stands (Jones et al. 2005). There are benefits and limitations to all of the approaches. Direct measurement from isolated individuals is by definition difficult for common and ecologically important tree species. The theoretical models require a detailed understanding of the properties of the dispersal agents (i.e., wind patterns, animal behavior). Inverse modeling in contrast, allows the parameterization of simple empirical models that encapsulate the basic processes that generate the observed patterns of seed production and dispersal. This approach, however, is data intensive and requires a large number of observations of seed rain in relatively large mapped stands (Canham and Uriarte 2006).

Previous studies using inverse modeling have generally focused on wind-dispersed species. In New Zealand forests, seeds of many dominant tree species lack specific adaptation for wind dispersal, and there is interest in whether there are predictable patterns of spatial variation in seed rain as a function of distance and direction from parent trees, and whether this spatial variation has implications for the distribution and abundance of vertebrate seed predators (Wilson et al. 2007), over and above the expected strong inter-annual temporal variation in seed production. In this study we use inverse modeling to characterize spatial and temporal variation in seed production and dispersal by four dominant tree species of southern temperate rainforests in New Zealand: the conifers rimu (*Dacrydium cupressinum*) and Hall's totara (*Podocarpus hallii*); and the angiosperms mountain beech (*Nothofagus solandri* var. *cliffortioides*) and silver beech (*N. menziesii*). In contrast to previous

studies that have assumed that all seed input results from local parent trees, we explicitly test for evidence of a 'bath' input of seeds originating from non-local source parents. This is likely to be more substantial for the bird-dispersed conifer species than for the wind- and gravity-dispersed angiosperms. Our approach also allows us to test critical assumptions about the relationship between tree size and reproduction.

## Methods

### *Study region and species*

As part of a detailed forest ecosystem study, seven study sites were established between the Waitutu River (46°14.4′ S, 167°3.9′ E) and the Crombie Stream (46°15.7′ S, 167°12.9′ E) catchments on the south coast of New Zealand's South Island in February 2001. The sites were distributed along a marine terrace sequence varying in age and soil fertility (Ward 1988, Mark et al. 1988, Coomes et al. 2005). Four sites were on uplifted marine terrace sites of intermediate fertility (~100 m above sea level [asl]) dominated by the conifers rimu (*Dacrydium cupressinum*), miro (*Prumnopitys ferruginea*), and Hall's totara (*Podocarpus hallii*), and the angiosperms silver beech (*N. menziesii*), mountain beech (*N. solandri* var. *cliffortioides*), kamahi (*Weinmannia racemosa*), and southern rata (*Metrosideros umbellata*). Three sites were on fertile alluvial surfaces (<40 m asl) of the Waitutu River and Crombie Stream, where the dominant canopy tree species were silver beech and kamahi, with scattered emergents of rimu and kahikatea (*Dacrycarpus dacrydioides*). The beeches, rimu and kahikatea are all considered 'masting' species while the other species produce more consistent seed crops. See Coomes et al. (2005) for an extended site description.

Total tree basal area ranged from 75 to 84 $m^2$ $ha^{-1}$ in the alluvial forests and 69 to 125 $m^2$ $ha^{-1}$ for the marine terrace forests (Coomes et al. 2005). Adult tree densities (i.e., for stems >10 cm DBH for canopy species, and >2.5 cm DBH for subcanopy species) were much lower on the alluvial sites (421–605 stems $ha^{-1}$) than on marine terraces (928–1661 stems $ha^{-1}$). Angiosperms were dominant on the alluvial sites both in terms of stem density (stems $ha^{-1}$) and total basal area ($m^2$ $ha^{-1}$).

### *Parent tree mapping*

At each study site, permanent plots of either 1.5 ha (East Crombie Alluvial [ECA], Slaughter Burn Alluvial [SBA], East Crombie Marine [ECM], Waitutu Marine [WM]) or 2.25 ha (West Waitutu Alluvial [WWA], East Waitutu Marine [EWM], West Crombie Marine [WCM]) were mapped in 2001 and 2002. Stems >10 cm DBH of all canopy species and >2.5 cm DBH of all subcanopy species in each plot were mapped from control points using an Impulse laser rangerfinder with digital inclinometer and compass (Laser Technology, Colorado, USA). Four of the tree species (rimu, miro, Hall's totara and kahikatea) are dioecious. Flowering of these tree species is irregular, making field determination of males versus females at this scale unrealistic. Therefore the sex of individuals of these species was not determined.

### *Seed collection*

We systematically established 10–15 seed traps (0.28 $m^2$) within the mapped stands at each site. Seed traps stood on wooden stakes approximately 1 m off the ground and had a metal circular frame and funnel-shaped netting basket to catch seed. Seed traps were cleared every three months and seeds were counted by species. Seed rain was collected from 2002 to 2009 in three main sites (EWM, SBA, and WWA), from 2003 to 2009 in one site (WM), and from 2002 to 2006 at the three Crombie Stream sites (ECA, ECM, and WCM), giving a total of 585 seed trap/year observations. No rodent feces were detected in the seed traps; therefore we assume predation from inside seed traps was negligible.

We have focused our analyses on the four tree species that were most abundant at these sites as both canopy trees and in seed collections: silver beech, mountain beech, rimu and Hall's totara. The seeds of the two beech species are three-winged or two-winged nuts, but the wings are poorly developed. Mature nuts vary from 5 to 7 mm long and the seeds weigh approximately 4 mg (Wardle 1984). Rimu and Hall's totara seeds are borne on top of a fleshy red aril and are bird-dispersed. Seed size varies from 3–4 mm long in rimu to 6–7 mm long in Hall's totara (Webb and Simpson 2001, Ruscoe et al. 2004).

Table 1. Comparison of alternative models for seed dispersal in the four tree species. NP is the number of parameters in the model, including the zero-inflation term. Delta $AIC_c$ is the difference in AIC (corrected for small sample size) between the best model (delta AICc = 0) and alternative models. Also reported is the goodness of fit ($R^2$) of the best model (including the best spatial and non-spatial models for silver beech).

| Species and model | NP | Delta $AIC_c$ | $R^2$ |
|---|---|---|---|
| Rimu (*Dacrydium cupressinum*) | | | |
| Model 0 (non-spatial) | 47 | 30505 | |
| Model 1 (alpha = 2, no minimum DBH) | 19 | 12792 | |
| Model 2 (vary alpha and minimum DBH) | 21 | 7842 | |
| Model 3 (Model 2 plus terrace-specific fecundity) | 29 | 0 | 0.169 |
| Hall's totara (*Podocarpus hallii*) | | | |
| Model 0 (non-spatial) | 47 | 595 | |
| Model 1 (alpha = 2, no minimum DBH) | 19 | 268 | |
| Model 2 (vary alpha and minimum DBH) | 21 | 0 | 0.676 |
| Silver beech (*Nothofagus menziesii*) | | | |
| Model 0 (non-spatial) | 47 | 0 | 0.206 |
| Model 1 (alpha = 2, no minimum DBH) | 19 | 12528 | |
| Model 2 (vary alpha and minimum DBH) | 21 | 4815 | |
| Model 3 (Model 2 plus terrace-specific fecundity) | 29 | 2749 | 0.249 |
| Mountain beech (*Nothofagus solandri* var. *cliffortioides*) | | | |
| Model 0 (non-spatial) | 47 | 3316 | |
| Model 1 (alpha = 2, no minimum DBH) | 19 | 999 | |
| Model 2 (vary alpha and minimum DBH) | 21 | 0 | 0.617 |

### Analysis

We used maximum likelihood estimation to fit both spatial and non-spatial models of seed rain within individual sites and years. The non-spatial models (Model 0, Table 1) simply estimated mean seed rain of a given species individually for each site and year combination (7 sites and 5–8 years per site). The spatial models incorporated information about the spatial locations of parent trees within each stand to estimate the parameters that define (1) the fecundity of individual trees as a function of their size, and (2) the shape of the dispersal curve as a function of distance. As with previous studies (i.e., Ribbens et al. 1994), we assume that the total seed production by an individual tree is a function of stem diameter $g$(DBH)

$$g(\mathrm{DBH}) = \mathrm{TSP}_y \left(\frac{\mathrm{DBH}}{30}\right)^{\alpha} \quad (1)$$

where $\mathrm{TSP}_y$ is the standardized total seed production of a 30 cm DBH tree in year $y$ (Ribbens et al. 1994, LePage et al. 2000, Uriarte et al. 2005) (Model 1, Table 1). For the two species that occurred frequently enough on both the fertile alluvial sites and the less fertile terrace sites (silver beech and rimu), we also tested a model (Model 3, Table 1) in which TSP varied with both year and site type (alluvial versus terrace). Following the arguments presented by Canham and Uriarte (2006), we test the assumption that fecundity is linearly proportional to biomass (fecundity $\sim$ biomass $\sim$ $\mathrm{DBH}^{\alpha}$, where $\alpha = 2$) by comparing a model fitted with $\alpha$ fixed at a value of 2 with a model that allowed $\alpha$ to vary. In that alternative model (Model 2, Table 1) we also included an additional estimated parameter ($\mathrm{DBH}_{\mathrm{min}}$) to determine the minimum size (DBH) at which potential parents began contributing to seed rain.

We tested two alternative forms—the lognormal and exponential functions—for the shape of the seed dispersal pattern. Many previous studies have assumed that seed density declines monotonically with distance from a parent tree, and have used some form of an exponential function (Ribbens et al. 1994, Clark et al. 1999, LePage et al. 2000):

$$f(d) = \frac{1}{\eta} e^{-Bd^{\beta}} \quad (2)$$

where $d$ is the distance from a seed trap to a parent tree, $B$ and $\beta$ are estimated parameters, and $\eta$ is a normalization constant equivalent to the arcwise integration of the dispersal kernel. Most previous studies have arbitrarily fixed $\beta$ at a value ranging from 1 to 3, but more recent studies (Uriarte et al. 2005, Canham and Uriarte 2006) have allowed $\beta$ to vary, allowing the data to determine the appropriate shape.

Greene et al. (2004) have shown that the lognormal dispersal function may be more appropriate for both wind- and animal-dispersed seeds. Thus, we also tested a lognormal function of the form:

$$f(d) = \frac{1}{\eta} e^{-\frac{1}{2}\left(\frac{\ln\left(d/X_0\right)}{X_b}\right)^2} \quad (3)$$

where $X_0$ is the distance at which maximum seedfall occurs (mode of the dispersal kernel), and $X_b$ determines the breadth or spread of the seedfall dispersal kernel. The lognormal model produced superior fits to the data (higher likelihoods and lower AIC) than the exponential functions for all of our species, so we do not present results from the exponential model below.

Finally, while previous studies of seed rain and seedling dispersion using inverse modeling have assumed that all input is local (i.e., originating from one of the potential parent trees within the mapping radius), other studies have suggested that seed rain should be analyzed in terms of both local input and a distance-independent "bath" of seed rain from both local and landscape-scale sources. We have tested for this form of non-local seed rain using a simple year-specific intercept in our model ($\text{bath}_y$ in Eq. 4, below).

Combining Eq. 1 with Eq. 3, the potential number of seeds ($S_{ymi}$) of a given species in seed trap $i$ in site type $m$ (alluvial vs. terrace) in year $y$ is:

$$S_{ymi} = \text{bath}_y + \text{TSP}_{ym} \sum_{j=1}^{n} \left(\frac{\text{DBH}_j}{30}\right)^{\alpha} f(d_{ij}) \quad (4)$$

where $\text{DBH}_j$ is the diameter of $j = 1, \ldots, n$ conspecific trees with diameter greater than $\text{DBH}_{\min}$ within the mapped stand, and $d_{ij}$ is the distance from the seed trap $i$ to tree $j$. Canham and Uriarte (2006) discuss issues related to the radius used to determine which parent trees to include in the analysis. The size of our mapped stands and the distribution of seed traps within those stands were designed to ensure that all parents within a minimum 20 m radius of each seed trap were mapped. In effect, all of the inverse modeling studies of seed and seedling dispersion have to deal with incomplete data sets in which some potential parent trees (due to low but non-zero long distance dispersal) are omitted from the analysis (Canham and Uriarte 2006). This has the potential to introduce bias in the parameter estimates, particularly for the TSP term. However, Canham and Uriarte (2006) have shown that the bias (particularly in the shape of the dispersal kernel) is low as long as the minimum mapping distance extends beyond the estimated mean dispersal distance. They also have shown that there are benefits in including the incomplete sample of additional mapped trees beyond the minimum complete mapping distance (Canham and Uriarte 2006).

We used likelihood estimation to fit both the spatial and non-spatial models, and assumed that the expected number of seeds in a seed trap follows a zero-inflated Poisson distribution in which the mean of the distribution is given by Eq. 4.

$$\text{Prob}(y_i|\theta) = \begin{cases} P_z + (1-P_z)\text{Poisson}(0|\theta) \text{ if } y_i = 0, \\ (1-P_z)\text{Poisson}(y_i|\theta) \text{ if } y_i > 0 \end{cases}. \quad (5)$$

The zero-inflation term ($P_z$) accounts for the larger-than expected number (under the Poisson distribution) of seed traps containing no seeds of a given species. Clark et al. (1999) have recommended the use of a negative binomial distribution to fit dispersal functions for heavy, animal-dispersed seeds for which there is a high degree of clumping. The negative binomial requires estimation of one additional parameter (a "clumping" parameter) that allows the variance to vary as a function of the mean. The negative binomial often produces models with higher likelihood because it can treat occasional extreme values as more likely than under a Poisson process. However, for the same reason, the negative binomial is very sensitive to the effects of even a few outliers (i.e., anomalously large numbers of seeds in just one or a few traps), and in our preliminary tests use of the negative binomial produced highly biased models (i.e., models in which the relationship between observed and predicted seed rain deviated sharply from a slope of 1).

We used simulated annealing (a global optimization algorithm; Goffe et al. 1994), to find the parameter values that maximized the likelihood of observing the recorded seed trap counts. Asymptotic 2-unit support intervals (roughly

analogous to 95% confidence intervals) were calculated for each maximum likelihood parameter estimate. The optimization was done with software written specifically for these analyses, using Delphi 7.0 (Borland Inc.). Alternative models were compared using AIC corrected for small sample size. The models were evaluated using two measures: bias in the models was assessed using the slope of the relationship between observed and expected seed rain, and $R^2$ was used as a measure of goodness of fit. To account for the zero-inflation term, these measures were calculated by randomly selecting and dropping a fraction $P_z$ of the zero counts, and calculating slope and $R^2$ on the remaining fraction of the data. This was repeated 1000 times, and the average slope and $R^2$ are reported.

## Results

For all four species, spatial models that estimated fecundity as a function of both tree size and an estimated minimum reproductive size were superior to simpler models that assumed that fecundity was a squared function of DBH and that all trees >10 cm DBH potentially contributed seeds (Table 1, Models 2 vs. 1). In addition, for the two species that occurred on both fertile alluvial and less fertile marine terrace site types, models that estimated separate fecundities by site type were superior to simpler models that averaged across the site types (Table 1, Models 3 vs. 2). For three of the four species (mountain beech, rimu, and Hall's totara) the spatial models were clearly superior to the non-spatial models (Table 1, Models 2 or 3 vs. Model 0). For silver beech, the species with the highest basal area of any species across the seven sites, the non-spatial model was superior to the best spatial model (Table 1, Model 0 vs. 3). The $R^2$ values for the best models for each species ranged from 17% to 68% (Table 1). Slopes of the relationship between observed and predicted (after accounting for the predicted zero inflated counts) were very close to 1 (unbiased) for three of the four species, but the best spatial and non-spatial models for silver beech were both slightly biased, with the models underestimating the observed counts (slope = 1.31 for the best non-spatial model, and 1.44 for the best spatial model; Table 1).

### *Size and site dependent variation in seed production*

The majority of previous studies using inverse modeling have assumed that during seed years all canopy trees contribute to seed production. In contrast, our analysis indicates that for the two conifers—rimu and Hall's totara—only the largest trees within each population contributed to seed production (Table 2). The estimated minimum size of the trees contributing to seed rain over the 8 years was 42.0 cm DBH for rimu and 55.7 cm DBH for Hall's totara. Trees greater than these minimum sizes represent 45% of rimu trees >10 cm DBH, but only 2% of Hall's totara trees >10 cm DBH. For both beech species the minimum reproductive size was lower but still well above the 10 cm lower limit of the mapped trees (22.4 cm DBH for mountain beech and 29.3 cm DBH for silver beech, representing 49% and 60%, respectively, of trees of those species >10 cm DBH). Previous studies have also typically assumed that fecundity increases as a squared function of DBH (i.e., $\alpha = 2$, and fecundity is therefore approximately linearly related to biomass). In our study, maximum likelihood estimates of $\alpha$ for the two beech species and Hall's totara were effectively zero (Table 2), indicating that there was no increase in fecundity with increasing DBH above the estimated minimum reproductive size. For rimu, the maximum likelihood estimate of $\alpha$ was 4.08, indicating that seed production per unit biomass increased very rapidly with increasing size. Combined with the large estimated minimum size for seed production, these results indicate that the very largest rimu and Hall's totara trees in the stands dominated seed rain of those two conifers over the period of our study (Table 2).

Two of the four species—silver beech and rimu—were common on both the fertile alluvial sites and the less fertile terrace sites. For both of these species, the model with different annual estimates of standardized total per capita seed production (TSP) on alluvial versus terrace sites was far superior (lower $AIC_c$) to the model that fit a single set of annual TSPs across all sites (Table 1, Models 3 vs. 2). The two species showed contrasting patterns, however, with the angiosperm (silver beech) having higher fecundity on the alluvial sites, while the conifer (rimu) had higher per capita fecundity on the terrace sites (Table 2).

Table 2. Maximum likelihood parameter estimates and two-unit asymptotic support intervals (in parentheses) for the best spatial models for the four tree species. Support intervals were not calculated for the $DBH_{min}$ parameter, because it was used as a threshold for determining which trees to include in calculation of local seed input. Separate sets of estimates of total seed production (TSP) were fitted for the two species, rimu and silver beech, that occurred in sufficient numbers on the two different terraces. For those two species, Terrace 1 was the fertile alluvial terrace sites and Terrace 2 was the infertile marine terraces.

| Parameter | Rimu (*Dacrydium cupressinum*) | Hall's totara (*Podocarpus hallii*) | Silver beech (*Nothofagus menziesii*) | Mountain beech (*Nothofagus solandri* var. *cliffortioides*) |
|---|---|---|---|---|
| Zero inflation term | 0.130 (0.099–0.158) | 0.575 (0.510–0.629) | 0.267 (0.232–0.308) | 0.595 (0.543–0.650) |
| $\alpha$ | 4.08 (4.07–4.09) | 0.00 (0.00–0.10) | 0.00 (0.00–0.00) | 0.17 (0.09–0.26) |
| $X_0$ (cm) | 3.04 (3.02–3.05) | 0.10 (0.10–0.10) | 3.05 (3.04–3.05) | 5.33 (5.28–5.37) |
| $X_b$ | 0.547 (0.545–0.550) | 1.548 (1.535–1.561) | 0.705 (0.704–0.705) | 0.439 (0.434–0.444) |
| $DBH_{min}$ (cm) | 42.00 | 55.72 | 29.25 | 22.39 |
| Bath seed input 2002 (no./$m^2$) | 137.11 (129.7–145.5) | 0.00 (0.0–0.2) | 34.41 (30.0–41.0) | 0.49 (0.1–1.7) |
| Bath seed input (no./$m^2$) | | | | |
| 2003 | 154.36 (146.7–161.2) | 16.93 (13.9–20.0) | 194.60 (192.7–195.9) | 132.74 (119.5–142.9) |
| 2004 | 2.47 (0.6–4.8) | 0.39 (0.0–1.5) | 0.00 (0.0–1.2) | 1.37 (0.5–2.7) |
| 2005 | 21.54 (18.3–24.5) | 0.68 (0.2–1.8) | 154.62 (147.1–164.3) | 47.19 (40.4–54.3) |
| 2006 | 5.83 (4.0–8.3) | 0.66 (0.1–1.6) | 26.12 (22.0–30.1) | 0.25 (0.0–0.8) |
| 2007 | 17.90 (13.1–22.3) | 0.71 (0.1–1.9) | 32.74 (28.6–38.3) | 0.00 (0.0–0.4) |
| 2008 | 24.05 (20.9–28.1) | 0.00 (0.0–1.1) | 28.86 (22.2–32.5) | 1.77 (0.8–3.6) |
| 2009 | 194.32 (186.4–205.3) | 5.83 (3.4–9.9) | 363.04 (349.6–374.7) | 52.45 (44.9–60.3) |
| Terrace 1 TSP | | | | |
| 2002 | 770.6 (728.0–826.0) | 0.00 (0.0–2280.0) | 40336.13 (38760.3–42769.5) | 44462.22 (42212.9–46569.6) |
| 2003 | 0.00 (0.0–1.9) | 24833.64 (14348.9–34974.7) | 105509.76 (105191.7–105739.1) | 30958.15 (28259.9–32693.7) |
| 2004 | 769.47 (712.0–823.9) | 102298.90 (87414.4–118614.1) | 4170.70 (3474.3–4864.2) | 13948.08 (12843.6–15397.1) |
| 2005 | 918.54 (877.7–975.2) | 115787.63 (101685.4–133691.6) | 129735.07 (126861.3–134017.6) | 18499.67 (17040.2–20150.7) |
| 2006 | 1316.13 (1240.2–1370.9) | 61345.20 (48509.7–76227.3) | 34342.24 (32708.7–36218.5) | 4397.80 (3555.0–5315.6) |
| 2007 | 246.10 (216.6–285.3) | 16053.92 (9679.1–25553.8) | 84023.32 (80840.6–87880.2) | 59695.26 (56796.3–62317.1) |
| 2008 | 183.04 (157.6–206.7) | 54367.63 (40229.5–69899.9) | 22126.12 (19446.2–24163.2) | 0.00 (0.0–326.2) |
| 2009 | 948.54 (900.0–1004.8) | 63648.48 (50765.4–80699.1) | 156997.36 (150589.1–161712.3) | 177243.47 (172664.4–181856.1) |
| Terrace 2 TSP | | | | |
| 2002 | 5470.31 (5349.7–5606.1) | | 0.00 (0.0–77.0) | |
| 2003 | 4216.28 (4112.7–4318.3) | | 4324.58 (3069.6–5272.3) | |
| 2004 | 380.87 (347.7–409.0) | | 2175.78 (1693.3–2749.8) | |
| 2005 | 1198.84 (1149.5–1252.1) | | 21948.55 (20879.9–23534.7) | |
| 2006 | 1813.06 (1749.5–1870.7) | | 1712.22 (1142.2–2206.8) | |
| 2007 | 244.93 (213.3–291.2) | | 0.00 (0.0–542.3) | |
| 2008 | 166.04 (137.4–203.8) | | 786.08 (0.0–1327.2) | |
| 2009 | 2673.46 (2561.9–2799.3) | | 13707.23 (11915.5–15839.3) | |

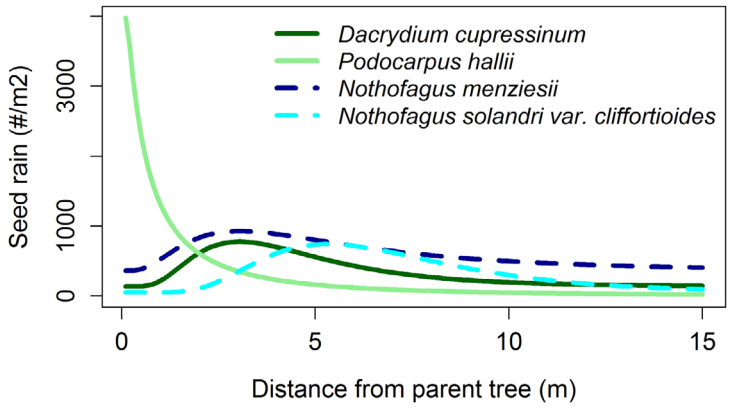


Fig. 1. Estimated dispersal functions around parent trees of the four species, combining both local and bath inputs. The functions are plotted using the TSP and bath input parameters from the year for each species that had the highest estimated total seed production (TSP), and are plotted for a 60 cm DBH parent tree.

### *Spatial variation in seed rain*

The spatial models decompose seed input at a trap location into two components: "local" seed rain as a summed function of the distance to individual parent trees within the stand (Eq. 3), and a "bath" term that is independent of the spatial distribution of potential parent trees. The dispersal functions estimated by the spatial models predict that the "local" seed rain was indeed highly localized, with modal dispersal distances of less than 6 m, and steep declines with increasing distance from a parent tree (Fig. 1). But our models estimate a large non-local (bath) input of seeds of the two most common tree species (the bath term for silver beech was 104.3 seeds/$m^2$ averaged across all eight years, and 69.7 seeds/$m^2$ for rimu). These two species also had the lowest average coefficients of variation in total seed counts across all seed traps within a given year (silver beech, mean CV for the eight years = 173%, rimu mean CV = 198%, versus 222% for silver beech, and 240% for Hall's totara). Bath input of seeds was intermediate for mountain beech (29.5 seeds/$m^2$ averaged over the eight years), and very low in Hall's totara (3.2 seeds/$m^2$ averaged over the eight years) (Table 2). The estimated bath seed input varied dramatically over time in concert with the temporal variation in estimated average fecundity (TSP) (Table 2 and Fig. 2B). As a percentage of total estimated or observed seed rain, the bath input was high during mast years, but very low during years of low seed rain (Fig. 2B).

### *Temporal variation in seed rain*

There was little synchrony across the four species in years of moderate to high seed rain (Fig. 2A), but two of the eight years (2004 and 2008) were characterized by very low total seed rain by the four species (Fig. 2A). The low total seed rain in 2004 and 2008 reflects the very low estimated average fecundity (TSP) in those years for the two most common species (rimu and silver beech) (Fig. 2C). Hall's totara, on the other hand, had moderate to high fecundity during those two years (Fig. 2C), but reproduction was limited to the very largest trees of that species, so the contribution of totara seeds to overall seed rain was very small.

The four species differed widely in both the frequency of large seed crops and the duration of intervals between years of high fecundity. Silver beech showed a consistent pattern of alternating years of low versus high fecundity (Fig. 2C). Mountain beech, in contrast, had one year (2009) with very high fecundity following a year (2008) with an almost complete seed crop failure, but the preceding six years were characterized by variable but low to moderate fecundity (Fig. 2C). Hall's totara showed a cyclical pattern with a five-year interval between years of very low fecundity (2002 and 2007), but the intervening years were characterized by very gradual interannual increases and then decreases (Fig. 2C). Rimu was characterized by two years of high fecundity (2002–2003), followed by five years of low to moderate fecundity (Fig. 2C).

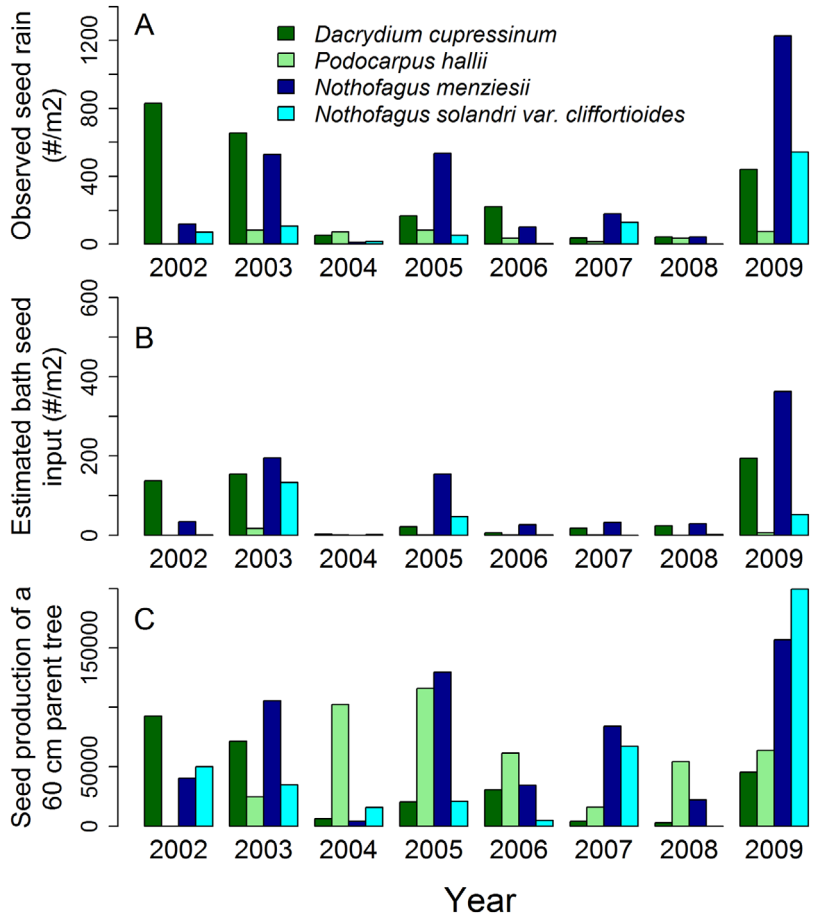


Fig. 2. (A) Observed seed rain (no./m$^2$, by species, averaged across all traps in all sites, by year). Note that seed rain for *P. hallii* was multiplied by 10 for display purposes. (B) Estimated bath seed input (no./m$^2$, by species, by year). (C) Estimated total number of seeds produced (TSP) and distributed locally (i.e., excluding contributions to the bath seed input), for a 60 cm DBH parent tree, by year. For the two species that occurred on both alluvial and marine terraces, TSP is shown for the terrace on which the species had highest fecundity (alluvial terraces for *N. menziesii*, and marine terraces for *D. cupressinum*).

## Discussion

### *Seed shadows and local versus bath seed input*

Both mountain and silver beech nuts have only rudimentary wings resulting in limited wind dispersal (Wardle 1984). In contrast, rimu and Hall's totara seeds are small and attached to an aril and rely primarily on birds for dispersal. Our results support the suggestions of Nathan and Muller-Landau (2000) that seed input be decomposed into both local neighborhood and long-distance processes. All four species showed evidence of a significant "bath" input of seeds that could not be attributed to parent trees within the immediate neighborhood (i.e., within 50 m). As suggested by Greene et al. (2004), the local seed shadows in both groups of species were best fit with a lognormal function rather than a monotonically declining exponential function. For three of the four species, peak seed rain occurred 3–6 m from the base, while in Hall's totara, local dispersal declined monotonically with distance beyond <1 m from a parent tree, but was still better fit by a lognormal seed shadow.

### *Individual-level variation in seed production*

Virtually all previous studies using inverse

modelling have arbitrarily assumed that individual levels of seed production vary as an approximately linear function of tree biomass (i.e., $\alpha = 2$; Ribbens et al. 1994, Clark et al. 1999), and that all trees above a low threshold DBH (10–15 cm) contribute to seed production. Greene and Johnson (1994) have summarized results from a wide range of empirical studies on plant fecundity using a relationship that is a linear function of tree basal area and a power function of seed mass. Early models fixed the $\alpha$ parameter in Eq. 1 because of computational difficulties in simultaneously estimating $\alpha$ and TSP. Canham and Uriarte (2006) have shown that the annealing algorithm that we used in this study is capable of simultaneously estimating both these parameter without tradeoffs as long as there is reasonable range of adult tree sizes (as was true for our study sites). Our results show that both previously invoked assumptions do not hold for the species we have examined. Similarly, a study of seedling dispersion patterns in a tropical rainforest concluded there was a large minimum size that trees had to obtain before significant seedling production occurred (Uriarte et al. 2005). Beyond this minimum size, both our study and the results of Uriarte et al. (2005) show two different patterns in the relationship between size and reproductive effort. In one set of species, there was very little relationship between tree size and reproductive effort above the minimum threshold. In the second pattern, not only was there a high minimum threshold for reproduction, but additionally the values of $\alpha$ were significantly greater than two, thus the largest trees contributed disproportionately to the seed crop. These results indicate that seed rain patterns will be even patchier than would be predicted simply from the size and distribution of all canopy trees.

### *Population-level variation in seed production*

Beyond individual patchiness in seed production within stands, our results indicate that there can be substantial population-level variation in fecundity among sites (as measured by standardized per capita production of seeds, TSP). Silver beech was characterized by large variation in seedfall among sites but showed consistently higher fecundity on the higher fertility alluvial sites. These results parallel those found by Davis et al. (2004) who demonstrated greater seed production in fertilized mountain beech stands compared with unfertilized controls. In comparison, TSP in rimu was higher on the marine terrace sites and in fact, individuals are more abundant on these less fertile terrace sites (Coomes et al. 2005). It is generally assumed that rimu (a conifer) is displaced from the more fertile alluvial sites by competition with beech and other angiosperms (Coomes et al. 2005). Our results suggest that rimu is more fecund on the marine terrace sites, and therefore bring into question whether they are indeed relegated there by competition, or rather are highly adapted to the less fertile marine terraces (Coomes et al. 2005).

It is worth noting that the inverse modelling methods estimate TSP as a population average on the assumption that all trees above a minimum threshold are reproductive. In reality, it is likely that in all of these species, not all individuals produce seed in a given year (Connell and Green 2000). This is particularly true for rimu and Hall's totara, which are dioecious. The functions we have parameterized will accurately predict the overall density of seed rain, but the actual spatial pattern will be even patchier than we predict as we cannot identify the specific individuals that reproduce in any given year. Indeed, analysis of spatial variation in seedling distribution at our study sites shows significant autocorrelation in seedling density at spatial scales of 5–10 m (roughly the size of a single tree crown) (E. F. Wright, *unpublished data*).

Although our study contains only eight years of data, it would be difficult to characterize the temporal variation in seed production of any of the four species in terms of classic 'masting' cycles with respect to predator satiation, i.e., a strongly bimodal (i.e., often either large or nil) distribution of inter-annual variation in seed production, with strong cross-species synchrony in years of high seed production (Schauber et al. 2002, Allen et al. 2012). Indeed, the clearest pattern of temporal variation in combined seedfall of the four species was the synchrony across species in years of very low seed production (2004 and 2008). Our results are in agreement with Allen et al. (2012), who found very little support for bimodality in seed crop size in a 43-year study of mountain beech seed production.

Norton and Kelly (1988) report 15 mast years in a 33-year record of rimu seed production, although six of the mast events immediately followed a previous mast year. We observed a similar pattern in the two successive years of high estimated rimu fecundity (2002 and 2003). Burrows and Allen (1991) observed large seed crops by silver beech in 6 of 18 years—our results show an even higher frequency of large silver beech seed crops (every other year).

### *Seed rain, seed predation, and predator satiation*

Variable, non-bimodal, asynchronous production of multiple species of edible seed is likely to generate irregular rodent outbreaks owing to either high seedfall from one tree species or moderate seedfall from a combination of species. Population increases of the most common rodents in forests on the New Zealand mainland, house mice (*Mus musculus*) and ship rats (*Rattus rattus*), often follow high seedfall of beech (King 1983, King and Moller 1997, Dilks et al. 2003) or rimu and other podocarps (Ruscoe et al. 2004, Harper 2005, Murphy et al. 2008). In intervening years when seedfall from most tree species is low, the combined supply of edible seed may be sufficient to maintain higher ambient rodent density than in forests dominated by a single tree species with bimodal masting dynamics. In a study of house mice in a forest mosaic, mice were more abundant in mixed podocarp–hardwood forest than in beech forest when their overall density was low (Choquenot and Ruscoe 2000). The authors concluded that higher general food availability in the mixed forest patches prevented the severe rodent population declines that can otherwise follow irruptions. Ship rats are also usually more numerous in mixed forests than in pure beech forest (King and Moller 1997).

Higher ambient rodent numbers in the years between irruptions may support larger mustelid populations in mixed forest than where a single masting species dominates, with increased threats to native species from both mammalian taxa. Rodent and consequently stoat (*Mustela erminea*) populations often grow and crash during the two years after heavy seedfall (King 1983, Murphy et al. 2008, King and Powell 2011). Large population increases by ship rats are less predictable than those of mice, and may follow unusual events such as consecutive high seedfall years (King 1983, Dilks et al. 2003, Murphy et al. 2008). These resource pulses generate complex cascades of events, as invertebrates (Fitzgerald et al. 1996) and birds (Murphy and Dowding 1995, Wilson et al. 1998, Fidler et al. 2008) also respond to high seedfall years and likely contribute to the rodent and stoat population increases (Murphy and Dowding 1995, Fitzgerald et al. 2004, Kelly et al. 2008). The predation rate on birds increases as the result of numerical (King 1983) and functional (Murphy et al. 2008) responses of stoats, and rodents also prey on native invertebrates (Fitzgerald et al. 1996, Ruscoe et al. 2013) and other small animals (King 2005). Relatively high ambient densities of rodents and stoats, prior to population increases and after population declines, may result in higher rates of predation on native species in mixed forests compared with simpler forests in non-outbreak years. For example, in beech forests kaka (*Nestor meridionalis*) breed only in years of high seed production, feeding their young on the unfallen seed prior to rodent and stoat population peaks (Wilson et al. 1998). The reproductive success of these birds may be reduced in forests where ambient rodent and stoat densities are high.

Variation in the quantity and quality of food resources in space and time also leads to variation in animal activity at the tree-neighborhood scale (Wilson et al. 2007). For example, in a year of high seedfall from beech and rimu (2003), high rates of seed predation and captures of mice were associated with locations beneath the crowns of trees of these species (Wilson et al. 2007). Spatial patterns of mouse activity may also change prior to seedfall, when mice prey on litter-dwelling invertebrates feeding on fallen male beech flowers (Fitzgerald et al. 2004). Flowering by other species such as rimu may invoke a similar cascade of events, but the spatial distribution of flower-fall from this dioecious species will differ from that of the monoecious beeches. However, although the foraging activities of mice may alter spatial patterns of seedling establishment, the supply of seed is predicted to satiate mice in most years of high beech seedfall, and therefore mice are unlikely to cause beech recruitment failure (Ruscoe et al. 2005*b*).

### *Conclusions*

The linkages between spatial and temporal variation in tree seed production and the population dynamics of introduced mammals in New Zealand forests have potentially important implications for populations of both native birds and trees. In contrast to expectations from classic masting theory, the mixed species forests we studied showed little temporal synchrony in seed production across tree species, and only weak evidence of distinct bimodality in seed crop size within species. The most distinctive aspect of temporal variation in seed production at the community level was the occurrence of very low seed rain of any species in two of the eight years of the study. Even within these two years, one of the species (Hall's totara) had high per capita seed production, but was rare enough in our study sites that its seeds contributed relatively little to total seed rain. Seed dispersal in all four of the species can be partitioned into a highly localized seed shadow, concentrated within 5 m around relatively few and typically very large canopy trees, and a "bath" term of longer-distance dispersal. Other research in our study sites shows that the highly localized component of seed rain produces distinct local patterns of activity by mammalian seed predators beneath the crowns of species with large seed crops (Wilson et al. 2007). Taken together, these results suggest that these mixed podocarp/angiosperm forests will have very different spatial and temporal dynamics of introduced mammals than simpler forests dominated by one or a few tree species.

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